Status of the name Odocoileus hemionus crooki (Mammalia: Cervidae)

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Abstract.—The present name of the desert mule deer (Odocoileus hemionus crooki) is based on a specimen collected in southwestern New Mexico near the Mexican border. This specimen was originally described as a new species (Dorcelaphus crooki) of black-tailed deer, not as a mule deer, because many of its characteristics are intermediate between mule deer and white-tailed deer. In the same publication, Dorcelaphus hemionus eremicus is described from western Sonora, Mexico, as a new subspecies of desert mule deer. A number of mammalogists believed the type specimen of crooki to be a hybrid between desert mule deer and Coues white-tailed deer (O. virginianus couesi), while others hypothesized it represented extremes of normal variation in mule deer. I have reassessed the type specimen of Dorcelaphus crooki and reaffirm that it is a hybrid, invalidating the use of the crooki subspecies name. Consequently, the oldest available name for the desert mule deer is O. h. eremicus.

Resumen.—El nombre actual del venado bura del desierto (Odocoileus hemionus crooki) se basa en un ejemplar colectado en el suroeste de Nuevo Mexico cerca de la frontera con México. E. A. Mearns describió este ejemplar como una nueva especie (Dorcelaphus crooki) de venado cola negra, no como un venado bura, debido a que muchos de sus caracteres son intermedios entre los del venado cola blanca y los del venado bura. En la misma publicación, Mearns describió también a Dorcelaphus hemionus eremicus del occidente de Sonora, México, como una nueva subespecie de venado bura del desierto. Un gran número de mastozoólogos ha considerado que el ejemplar tipo de crooki es un híbrido entre el venado bura del desierto y el venado cola blanca de Coues (O. virginianus couesi), mientras que otros han hipotetizado que representaba extremos de la variación normal del venado bura. Después de reevaluar el ejemplar tipo de Dorcelaphus crooki concluyo que es en realidad un híbrido. Por lo tanto, el nombre válido más antiguo para el venado bura del desierto es O. h. eremicus.

Desert mule deer (presently known as *Odocoileus hemionus crooki* Mearns, 1897) inhabit the southwestern United States from West Texas through southern New Mexico and southern Arizona, and southward into Sonora, Chihuahua, Coahuila, Zacatecas, and Durango, Mexico (Leopold 1959, Cowan 1961, Wallmo 1981). In addition, a small herd has been translocated to Nuevo León, Mexico (Morrison et al. 1992; Fig. 1). Since its original description, the subspe-

cific name of this taxon has been contentious due to uncertainties regarding the hybrid status of the type specimen.

Historical Review

Mearns (1897) described *Dorcelaphus crooki* as a new species of black-tailed deer because of its similarity to the Columbian black-tailed deer (*O. h. columbianus*). The type specimen (National Museum of Natu-



Fig. 1. Current distribution of desert mule deer in the southwestern United States and northern Mexico. Type localities identified for a) *Dorcelaphus hemionus eremicus* Mearns, 1897; b) *Dorcelphus crooki* Mearns, 1897; and c) *Odocoileus hemionus canus* Merriam, 1901.

ral History [USNM] 20572/35752) was collected in 1892 by E. A. Mearns on the summit of the Dog Mountains, Hidalgo County (formerly part of Grant Co.), New Mexico during the survey of the boundary between Mexico and the United States. No other deer with similar characteristics were collected at or near that locality.

In the same publication Mearns (1897) described the "Burro deer or desert mule deer," *Dorcelaphus hemionus eremicus* based on a male (USNM 63403, the type) collected in 1895 by W. J. McGee in the Sierra Seri, Sonora, Mexico. McGee did not keep the skull, but processed the hide as a deer skin rug. Mearns (1897) described the subspecies as pale gray in color with short pelage, a dark dorsal stripe, paler forehead markings, and wide, heavy ant-

lers. This description was based on the skin of the male and two sets of antlers, each from different deer; one of which came from the Sonoyta Valley, Sonora (USNM 59910), the other from Black Butte, Baja California (USNM 60855). Pieces of skin trimmed from the hide as it was made into a rug comprised the only material representing the type specimen in the National Museum until 1902 when the rug was acquired from Anita McGee (Poole & Schantz 1942).

In 1901, Merriam described *Odocoileus hemionus canus* based on a male (USNM 99361) from Sierra en Medio, Chihuahua, Mexico. Merriam (1901) distinguished *O. h. canus* from the western subspecies *O. h. eremicus* solely on the basis of antler conformation. The Sierra en Medio lies only 40 km southwest of the type locality for *Dor*celaphus crooki in New Mexico.

In his list of big game of North America, and replacing *Dorcelaphus* with the correct senior synonym *Odocoileus*, Seton (1898: 286) included *O. h. eremicus* as a subspecies of mule deer, but maintained the "Crook black-tailed deer" as *O. crooki*. Lydekker (1915) also listed this animal as a black-tailed deer, *O. columbianus crooki*. Following Merriam's (1901) description, *O. h. canus* was used for the desert mule deer in West Texas, Arizona, New Mexico, and northcentral Mexico (Seton 1909, Lantz 1910, Lydekker 1915, Bailey 1931, Cowan 1936, Cahalane 1939, Dalquest 1953).

Several mammalogists believed that crooki was based on a hybrid between Coues white-tailed deer (O. virginianus couesi) and a desert mule deer but lacked known hybrids for comparison (Lydekker 1898, Seton 1929, Bailey 1931, O'Conner 1939). Goldman & Kellogg (1939) examined the holotype of O. h. canus and other specimens from the Sierra en Medio, Chihuahua, along with the holotype of Dorcelaphus crooki, and concluded that the type of crooki was an unusual specimen of mule deer and not a hybrid. Because the name crooki antedates canus, they adopted O. h. crooki as the correct name for desert mule deer in the north-central states of Mexico and adjacent Arizona, New Mexico, and Texas. Hoffmeister (1962) also re-examined the type of crooki and compared it with specimens of O. virginianus and O. hemionus. He interpreted the specimen as simply a mule deer with some features that were intermediate with or shared by whitetailed deer.

Based on the type specimen from Sierra Seri, the range of *O. h. eremicus* was designated somewhat arbitrarily as western Sonora, southwestern Arizona, and extreme southeastern California (Mearns 1907:210). Hoffmeister (1962) listed *O. h. eremicus* as a synonym of *O. h. crooki* because he did not consider western Sonoran mule deer (burro deer) distinguishable from other populations of desert mule deer. Only Cowan (1936, 1961) and Longhurst & Chattin (1941) attempted to quantify differences between deer within the ranges of eremicus and crooki. Cowan's (1936) interspecific cranial distinctions were based on only four eremicus skulls; of the two additional eremicus specimens from Mexico that he used to differentiate external characteristics, one was from Tiburon Island, Sonora, which Cowan (1961) later considered to be a different subspecies (O. h. sheldoni). Cowan (1961) based his differentiation of eremicus on measurements of only one male and one female specimen, which may have been previously described (Cowan 1936, Longhurst & Chattin 1941). Longhurst & Chattin (1941) added descriptions of pelage variations to differentiate eremicus, but they had only one crooki skin and three skulls for comparison. Cowan's (1936:236) measurements of eremicus from southwestern Arizona and California are within the normal variation of crooki reported by Hoffmeister (1986). Hall (1981) continued to treat western Sonoran mule deer as a separate subspecies (O. h. eremicus), but provided no supporting information. Hoffmeister (1962) found mule deer from southern Arizona and northern Sonora within 80 km of the type locality of O. h. eremicus (Sierra Seri, Sonora) to be sufficiently similar to warrant treating eremicus as a synonym of crooki. Hoffmeister (1986), while remarking that he could not confirm that O. h. eremicus was a synonym of O. h. crooki, still implied that western Sonoran mule deer were not distinguishable from those farther east. The purpose of this study is to confirm hybrid status of the type specimen for O. h. crooki and clarify subspecific nomenclature for desert mule deer.

Material and Methods

I re-examine the type specimen of *O*. *h*. *crooki* to compare and contrast its qualitative and quantitative characters with corresponding features of mule deer, white-tailed

deer, and their hybrids from southern Arizona, southern New Mexico, and adjacent Mexico. Published data from previous comparisons are supplemented by measurements (in millimeters) from female O. h. crooki (n = 12), female O. v. couesi (n =17), the type specimen of Dorcelaphus crooki, and a known O. h. crooki \times O. v. couesi F₁ hybrid. The type is an adult female, thus I included only adult females $(\geq 2 \text{ years old})$, as determined from tooth wear and replacement (Robinette et al. 1957, Severinghaus 1949), for comparison. Cranial measurements (Table 1) include the six used by Hoffmeister (1962, 1986) in addition to depth of lacrimal fossa (determined as either shallow, deep, or "no decision" by Hoffmeister 1962). All cranial measurements were taken with a metric dial caliper and recorded to the nearest 0.1 mm. Values for paired measurements (e.g., length of right and left nasals) are averages. Elsewhere in this report, I use the term hybrid to refer to only verified O. h. crooki \times O. v. couesi F_1 hybrids, unless otherwise noted.

Review of Characters

Hoffmeister (1962) reviewed characteristics useful for distinguishing O. virginianus and O. hemionus in Arizona in his evaluation of the type of crooki. These included cranial and external measurements (including size of metatarsal gland) along with qualitative descriptions of the type of antler, lacrimal pit, color pattern of the tail, and color and position of the metatarsal gland. He relied heavily on size because desert mule deer are larger than Coues whitetailed deer. Nevertheless, Hoffmeister did not have adults of known hybrids available to evaluate their size characteristics when deciding on the taxonomic status of the type of crooki. Although acknowledging Nichol's (1938) success in producing hybrids in captivity, Hoffmeister (1962:52) tended to discount the occurrence of hybrids in the wild. Today, however, data on dimensions

and other characteristics are available for mule deer \times white-tailed deer hybrids, including both captive produced and genetically confirmed, wild-taken animals. Characteristics of known hybrids produced in captivity provide a morphological basis for assessing suspected hybrids between mule and white-tailed deer encountered in the wild. The primary features used to distinguish between desert mule deer and Coues white-tailed deer concern the length and color pattern of the tail; size, position, and color of hair tuft of the metatarsal gland, depth of the lacrimal pit, and dimensions of the body and cranium (Table 1). My evaluation of the holotype of crooki based on these features follows.

Metatarsal glands.—Metatarsal glands of desert mule deer are positioned high on the metatarsus, exceed 75 mm in length, and are circumscribed with brown hair (Caton 1877, Hoffmeister 1986). Those of Coues white-tailed deer are positioned below the midpoint of the metatarsus, measure 25 mm or less in length, and are rimmed by white hairs (Quay 1971, Hoffmeister 1986). Unlike either parent, all known F₁ hybrids have metatarsal glands that are intermediate in length, location, and appearance (Table 2). As affirmed by Mearns (1907) and Bailey (1931), the position of the metatarsal gland in the holotype of crooki is intermediate in comparison to its location in white-tailed and mule deer (Fig. 2). It is nearly identical in location, length, and appearance to metatarsal glands of F₁ hybrids produced in captivity (Day 1980) and to wild mule \times white-tailed deer hybrids whose status was confirmed genetically (Wishart 1980).

The metatarsal glands of the type of *crooki* (right = 34 mm, left = 42 mm) are longer than those of white-tailed deer (25 mm or less) and well below the range for desert mule deer (75–150 mm; Table 1). Day's (1980) measurements of the metatarsal glands of two adult hybrids born in captivity were 50 mm for a female and 73 mm for a male. Wishart (1980) reported lengths

of glands from two wild-taken mule \times white-tailed deer hybrids (status confirmed by electrophoresis) as 50 mm for a female and 62 mm for a male. Halloran & Kennedy (1949) and Lang (1957:14) gave lengths of metatarsal glands of adult female desert mule deer from southern New Mexico that averaged 2 to 3 times the length of the gland in the holotype of *crooki*.

Anderson et al. (1964) included the corona of hair (circumglandular hair tuft) in their measurements of the metatarsal glands of 431 adult female mule deer from the Sacramento and Guadalupe mountains of southern New Mexico. Metatarsal gland lengths of females from the Sacramento Mountains (identified as *O. h. hemionus*) averaged 138 mm (range, 100–190); those of the Guadalupe Mountains (identified as *O. h. crooki*), 131 mm (range, 90–190). The shortest (90 mm) is considerably longer than the longest circumglandular hair-tuft measurement (70 mm) on the type of *crooki*.

Mearns (1897, 1907) described the hairs surrounding the metatarsal gland of the type of crooki as "sooty at the base and white apically." On examination, these hairs are "sooty at the base;" however, while pale, they are not white apically (Fig. 2c). Instead they are nearly the same pale color as the remainder of the leg, which Mearns (1897, 1907) described as "cream-buff, except where new clay colored hair is coming in on the anterior border." Metatarsal glands of hybrids produced in captivity are either circumscribed with white hairs (G. I. Day, in litt.) or the hairs match the brown coloration of their mule deer parent (J. C. Haigh, in litt.).

Tail.—Mearns (1897:2) described the tail of *crooki* as "colored much as in *D. columbianus*, but has a longer terminal switch; upper side and extremity of tail all black, lower side white medially, and naked towards the base" (Fig. 3c). He gave its vertebral length as 195 mm, which is longer than that of a female hybrid (184 mm; G. I. Day, in litt.) and in the range of *O. v.*

couesi, but at or exceeding the upper limit for desert mule deer (Table 1). The color pattern of the tail of the type of crooki resembles the tails of captive-born hybrids, which Day (1980) described as "dark reddish-brown or reddish-black above with white beneath and along the borders" (Fig. 3d). Tails of some subspecies of mule deer (e.g., O. h. fuliginatus) commonly have a dark dorsal surface; however, this pattern is rare in southern Arizonan and New Mexican populations. Of 349 desert mule deer observed in southeastern Arizona during January 1998, no adults had dark tails resembling the type of crooki. However, in areas of sympatry with white-tailed deer, two fawns seen in the company of female mule deer each had a wide, dark tail stripe. I do not know if these were hybrids or pure mule deer fawns; yet hybrid fawns are typically seen in the company of mule deer (Wishart 1980, Kay & Boe 1992), implying that the usual hybrid cross is between an aggressive white-tailed buck and a mule deer doe.

Length of hind foot.—Hoffmeister (1962, 1986) allowed that the length of hind foot (400 mm) of the *crooki* type is more characteristic of white-tailed deer. Based on the data at hand (Table 1), 400 mm is at the upper extreme of length of hind foot for Coues white-tailed deer and at the lower extreme for desert mule deer. G. I. Day's (in litt.) measurement of the length of hind foot in a captive-born hybrid is 405 mm.

Total length.—The total length of the type of crooki (1440 mm; Mearns 1897) and that of a female hybrid (1549 mm; G. I. Day, in litt.) is within the range for desert mule deer, but longer than normal for Coues white-tailed deer (Table 1). The ratio of tail length to total length for the type of crooki is $7.4 \times$ which is at the upper extreme for Coues white-tailed deer; however, the ratio in Day's female hybrid is $8.4 \times$ and within the normal range for desert mule deer (Table 1). The ratio deer (Table 1). The ratio deer (Table 1). The range of ratios of tail length to total length in Coues white-tailed deer is $5.6 \times -7.5 \times$, whereas the normal range of

Table 1.—Comparison of Coues white-tailed deer (*Odocoileus virginianus couesi*), desert mule deer (*O. hemionus crooki*), and an *O. virginianus couesi* \times *O. hemionus crooki* F_1 hybrid, and the type specimen of *Dorcelaphus crooki*. All measurements (in millimeters) are from adult females two years of age or older. Characteristics of the type of *Dorcelaphus crooki* from Mearns (1907); cranial measurements from A. L. Gardner (in litt.). Measurements of known hybrid (UA 22358) supplemented by morphological information from G. I. Day (in litt.). Sample sizes in parentheses.

Character	O. v. couesi	F ₁ hybrid	Type of <i>crooki</i>	O. h. crooki	Interpretation of <i>crooki</i> type		
Metatarsal gland:							
Location	Below midpoint of shank ^a	Intermediate	Intermediate	At or above mid- point of shank ^a	Hybrid		
Length	Usually <25 ^a 14–23 (4) ^b 18 (1) ^d	50	34R, 42L ^m	$75-150^{a}$ 102-121 (4) ^c $\bar{X} = 132^{e}$	Hybrid		
Length hair tuft			70	90–190 (431) ^f	Hybrid		
Color hair tuft	White ^{a,g}	Brown or white	Pale brown	Buff or Brown; never white ^{a,g}	Hybrid		
Tail: Length	215-260 (3) ^h	184	195	170–228 (5) ^h	Mule deer or Hybrid		
	>188 ^a 170–230 (9) ^d			145–180 (8) ^a 152–191 (5) ^c 165–229 (8) ⁱ 127–185 (8) ^j			
Dorsal color	White border, dull cinnamon ^h Gray, reddish- brown, grayish brown or almost black ^a	Dark reddish- black ^d Like white- tailed deer ^k	Black	White with black terminal brush ^h No white border, usually without midband ^a	Hybrid		
Length of hindfoot	$387-390 (3)^{h}$ <404 ^a $\bar{X} = 409^{e}$ $332-405 (18)^{d}$	405	400	430–464 (5) ^h 380–490 (448) ^f 406–445 (5) ^c 406–475 (8) ^a	Hybrid		
Total length	1410–1450 (3) ^h 1230–1420 (18) ^d	1549	1440	1370–1570 (5) ^h 1346–1549 (5) ^c 1397–1702 (8) ¹ 1430–1582 (8) ^j	Mule deer or Hybrid		
Ratio of tail to total length	$5.6 \times -6.6 \times (3)^{h}$ $5.9 \times -7.5 \times (9)^{d}$ $6.4 \times -7.3 \times^{m}$ $\bar{X} = 5.7 \times^{e}$	8.4 ×	7.4 ×	$\begin{array}{l} 6.0 \times -8.9 \times (5)^{\rm h} \\ 8.2 \times -10.5 \times^{\rm m} \\ 8.1 \times -10.2 \times (5)^{\rm c} \\ \bar{X} = 8.0 \times (8)^{\rm i} \\ \bar{X} = 10.1 \times^{\rm e} \end{array}$	Hybrid		
Depth of lacrimal	$3.0-5.7 (4)^{n}$	5.3	5.9R, 6.3L	6.4–11.2 (11) ⁿ Deep ^{a,h}	Hybrid		
Length of ear	<172 ^m 145–170 (18) ^d	188	190	190–193 (2) ^h 184.2–203.2 (5) ^c 175–220 (8) ^a	Mule deer		
Basilar length	205–216 (4) ⁿ 190.9–216.2 (13) ^o	222	229°	194.7–209.6 (8) ¹ 239–265 (7) ⁿ 230–246 (12) ^a	Hybrid		
Length of nasals	71.3–79.8 $(5)^{n}$ 60.4–76.7 $(13)^{o}$ 56.4 (51.0 (2))	72.0	80.7°	79.1–95.6 $(8)^n$ 79–95 $(4)^h$	Mule deer		
Orbital width	$55.3-59.7 (5)^{n}$ $54.5-56.0 (4)^{a}$	63	64.2°	$\begin{array}{c} 62.3 - 81.7 \ (12)^{a} \\ 65.7 - 79.8 \ (10)^{n} \\ 68.0 - 81.0 \ (12)^{a} \end{array}$	Hybrid		

Table 1.—Continued.

Character	O. v. couesi	F ₁ hybrid	Type of <i>crooki</i>	O. h. crooki	Interpretation of crooki type		
	51.5–62.2 (13)°						
	51.4-60.8 (2) ^p						
Zygomatic width	87.8-97.7 (6) ⁿ	96.3		99.1-113.7 (9) ⁿ	Mule deer		
	90–97 (4) ^a		102.1°	100–110 (13) ^a			
	89.4–100.4 (11)°						
	96.6-100.7 (2) ^p						
Length of upper P-M	63.5-67.2 (5) ⁿ	70.5		72.1-82.6 (11) ⁿ	Mule deer		
toothrow	61.1-69.6 (13)°		76.4°	80-89 (4) ^h			
	63.4-66.8 (4) ^a			70.1-85.5 (12) ^a			
Length of lower P-M	72.5-76.2 (3) ⁿ	80.7		80.9-100.5 (10) ⁿ	Mule deer		
toothrow	66.1–77.6 (11)°		87.2°	87-97 (4) ^h			
	72.1-74.4 (2) ^a			82.4–97.4 (12) ^a			
Usual topographic elevation (m)	1231-21549		above 1800	<1400 ^r	White-tailed deer		

^b Quay 1971.

^e Halloran & Kennedy 1949.

- ^d G. I. Day, in litt.
- ^e Lang 1959.
- ^f Anderson et al. 1964.
- ^g Caton 1877.
- ^h Mearns 1907.
- ⁱ Cowan 1961.
- ^j J. C. Truett, in litt.
- ^k Nichols 1938.
- ¹Bailey 1931.
- ^m Hoffmeister 1962.
- ⁿ This study.
- ° A. L. Gardner, in litt.
- ^p Krausman et al. 1978.
- ⁹ Anthony & Smith 1977.
- ^r Krausman 1978.

ratios in desert mule deer is $7.7 \times -10.5 \times$ (Mearns 1907, Hoffmeister 1962, G. I. Day, in litt.). An exception is a desert mule deer from west of El Paso, Texas (Mearns 1907), with an unusually long tail (228 mm) and short total length (1307 mm) yielding a ratio of $6.0 \times$.

Length of ear.—Total length of ear for the type specimen of O. h. crooki (190 mm) is within the normal range for desert mule deer and is longer than that of a white-tailed deer (Table 1). The length of ear for two adult F_1 hybrids (O. h. crooki \times O. v. couesi) was 188 mm (female), and 209 mm (male), also within the normal range for mule deer (G. I. Day, in litt.).

Lacrimal fossa.—Depth of the lacrimal

fossa is diagnostic; it is deeper (6.4-11.2 mm) and larger in desert mule deer than in Coues white-tailed deer (3.0-5.7 mm). Hoffmeister's (1962:49) "no decision" on the depth of the fossa in the type specimen of crooki was because both fossae are fenestrate. However, the floor of each fossa is clearly evident and the depth of the right fossa measures 5.9 and the left fossa, 6.3. These measurements are intermediate between the ranges of lacrimal-fossa depths of the two species and confirms Wishart's (1980) observation for known mule \times white-tailed deer hybrids. Depth of lacrimal fossa in another hybrid doe measures 5.3 (Table 1), which is near the upper range of that for white-tailed deer.

Table 2.—Comparison of length of metatarsal gland reported for the type specimen of Dorcelaphus crooki, several subspecies of mule deer (Odocoileus hemionus), and for known mule deer X white-tailed deer hybrids. Measurements (in millimeters) from adult females two years of age or older, unless otherwise noted.

ursal gland theses) Source	(よよ) Wishart 1980	(よよ) Day 1980	Hoffmeister 1962	Lang 1957	Hoffmeister 1962	1) Halloran & Kennedy 1949	Longhurst & Chattin 1941	Cowan 1961	5) Cowan 1936	Longhurst & Chattin 1941	Cowan 1936	Cowan 1936	Cowan 1936	Cowan 1936	Cowan 1936
\bar{X} length of metata (range in parent	50 (99), 62	50 (99), 73	34R, 42L	132	(75 - 150)	110 (102-121	110	114	108 (101-116	162	95 (90-100)	90 (89–91)	78 (65–93)	51 (35-84)	44 (41–51)
и	5	2	1			4	-	7	2	-	б	0	ŝ	14	3
Scientific name	0. virginianus \times 0. hemionus	0. v. couesi \times 0. h. crooki	Type of crooki	O. h. crooki			O. h. hemionus			O. h eremicus	O. h. peninsulae	O. h. californicus	O. h. fuliginatus	O. h. columbianus	O. h. sitkensis
Common name of subspecies	White-tailed \times mule deer F ₁ hybrid	Coues white-tailed \times desert mule deer F ₁ hybrid	Crook's blacktail	Desert			Rocky Mountain			Burro	Peninsula	California	Southern	Columbian black-tailed deer	Sitka black-tailed deer



Fig. 2. Metatarsal glands of: a) desert mule deer (*Odocoileus hemionus crooki* [=*eremicus*]); b) Coues whitetailed deer (*O. virginianus couesi*); c) holotype of (*Dorcelaphus crooki*, USNM 20572/35752); d) known F_1 hybrid (*O. h. crooki* × *O. v. couesi*). Photographs by J. R. Heffelfinger (a & b), L. M. Snyder (c), and G. I. Day (d).



Fig. 3. Tails of: a) desert mule deer (*Odocoileus hemionus crooki* [=*eremicus*]); b) Coues white-tailed deer (*O. virginianus couesi*); c) holotype of (*Dorcelaphus crooki*, USNM 20572/35752); d) known F_1 hybrid (*O. h. crooki* × *O. v. couesi*). Photographs by J. R. Heffelfinger (a & b), L. M. Snyder (c), and G. I. Day (d).

Cranial measurements.—Hoffmeister's (1962, 1986) decision that the type of crooki was a mule deer pivoted on the use of skull measurements. Adult desert mule deer in the region of the type locality of crooki are much larger and may weigh twice as much as Coues white-tailed deer resulting in some cranial dimensions being interspecifically diagnostic. Hoffmeister (1962:48) provided generalized interspecific limits, but not actual ranges of the six measurements (basilar length of Hensel, length of nasals, orbital width, zygomatic breadth, and length of both upper and lower molariform toothrows) he used in separating female mule and white-tailed deer. He said all six measurements of the type specimen for crooki were within the lower range of these measurements for desert mule deer. However, I found that orbital width and basilar length were below the corresponding ranges for this measurement for mule deer; the remaining four measurements were within the normal range. The discrepancy between Hoffmeister's (1962) measurement of the nasals of the type of crooki and the longer measurement in Table 1 credited to A. L. Gardner results from Hoffmeister's measurement equaling the shortest distance from the frontal-nasal suture to the proximal margin of its anterior border between medial and lateral anterior projections. Gardner's measurement is the average of the greatest distance between anterior and posterior points of right and left nasals; the right nasal measures 80.0 mm and the left, 81.5 mm. Hoffmeister's (1986) principal components analysis using 11 cranial measurements grouped measurements of the type of crooki with those of mule deer. Cranial measurements of an adult captiveborn hybrid doe are either intermediate or within the normal range for mule deer (Table 1).

Cowan (1962) reported four cranial dimensions (width of nasals, interorbital width, palatal width, and postpalatal width) used to differentiate mule deer and whitetailed deer in Alberta, Canada. Three of these four measurements from a male mule \times white-tailed deer hybrid (as determined from metatarsal gland characteristics) were within the normal range for mule deer. Wishart (1980) used five cranial measurements in an analysis of a male and a female wild-taken hybrid (both confirmed by electrophoresis) in Alberta. All measurements fell within the normal range for mule deer with the exception of post-palatal width of the female, which was within the range for white-tailed deer.

Type locality.—Mearns (1897, 1907:190) collected the type of *Dorcelaphus crooki* on 9 June 1892, on the summit of "Emory Peak of the Dog Mountains, where I noted its range as from 1500 to 1868 meters." Mearns (1907:87) was camped at "Dog Spring . . . [which] is about 2 kilometers . . . north of [Boundary] Monument No. 55 ... near the south extremity of the Dog Mountains, a rugged range of which Emory Peak, having an altitude of 1868 meters (6129 feet), is the highest." Dog Spring (31°21'N, 108°19'W) appears on several old maps as "Ojo del Perro." The Dog Mountains are known today as the Alamo Hueco Mountains. Apparently, the name Emory Peak does not appear on any topographic map of the area produced from 1881 through 1983 (C. Kollen, pers. comm.). A Department of the Interior, General Land Office map dated 1903 shows an "Emory Sp." northwest of Ojo del Perro, in the general vicinity of Pierce Peak (31°27'N, 108°20'W). As Pierce Peak is drained to the north by Emory Canyon and 11 km northwest of Dog Spring, it is most likely the same peak identified by Mearns as Emory Peak. The elevation of Pierce Peak is given today as 1877 m; however, a map of the area dated 1942 has the elevation as 6149 ft (1874 m). Mearns' (1907) elevation of 1868 m for Emory Peak is nearly equivalent; furthermore, Pierce Peak is covered with alligator juniper (Juniperus deppeana), which matches his description of the area.

The elevation at which the type of *crooki* was collected, presumed to be above 1800

m, is above the normal upper elevational limit for desert mule deer (1400; Krausman 1978, McCulloch 1972). Coues white-tailed deer, however, often occur in highest densities between 1230 and 2150 m elevation (Anthony & Smith 1977). Both species are present in the Alamo Hueco Mountains, but white-tailed deer are less common today than they were earlier in this century (Bailey 1931; Raught 1967; A. Hurt, pers. comm.).

Discussion

In the original description of *Dorcelaphus crooki*, Mearns (1897:3) said "The skull has very nearly the same conformation as that of *D. columbianus* [black-tailed deer], the lacrimal fossa being deeper than in the Virginia deer, but shallower than in the mule deer. The same intermediate condition obtains with respect to the vomer, in the relationships of the nasal and premaxillary bones, in the form and size of the teeth; and, in short, the whole animal appears to be a compromise between the characteristics of the white-tailed and mule deer."

In 1907, Mearns referred to this taxon as Odocoileus crooki and explained naming the deer for General George Crook. Mearns also received a specimen of a 2-year-old buck shot in the vicinity of Bill Williams Mountain, Arizona, in 1884 by a member of General Crook's hunting party. Mearns believed this specimen also represented his new species of black-tailed deer. I have not examined the male to verify its hybrid status because its identity has no bearing on the status of the name crooki because it is not the type. Mearns (1907:187) reported the length of metatarsal gland on this specimen as 13 mm, which is typical of a whitetailed deer (Table 1).

For several decades following Mearns' (1897) description of *Dorcelaphus crooki*, several authorities suggested that the type was a hybrid (Lydekker 1898, Seton 1929, Bailey 1931, O'Conner 1939) and Merri-

am's name O. h. canus was used for the desert mule deer. Goldman & Kellogg (1939), having noted that a mule deer (O.h. peninsulae) from lower Baja California, Mexico, had a tail color pattern similar to that of the type of crooki and reasoning that their animal could not be a hybrid because white-tailed deer were not in Baja California, concluded that the type of crooki was an abnormal specimen of mule deer. Hoffmeister (1962, 1986) acknowledged that the type of *crooki* was intermediate in some features, but believed the preponderance of evidence, particularly of size, supported his assessment that the animal was simply an abnormal mule deer. He also said that the metatarsal gland may be small or indistinct in some populations of mule deer elsewhere, citing Hershkovitz's (1958:538) observation that two mule deer from lower Baja California, Mexico, had poorly-developed glandular tissue underlying well-defined metatarsal hair tufts. Nevertheless, the type specimen of *crooki* has shortened metatarsal glands and circumglandular tufts unlike those of any known mule deer, but consistent in size, form, and position with those of known hybrids (Tables 1 & 2). Hoffmeister (1962:52), in his statement "The few 'hybrids' that I have been able to track down either prove to be clearly O. hemionus or O. virginianus," implied that hybridization between these species probably did not occur in the wild.

White-tailed deer \times mule deer hybrids are known to have been produced in captivity as early as 1865 (Gray 1972). Other examples of hybridization have been documented at captive facilities in Arizona (Nichol 1938, Day 1980), Colorado (Spraker et al. 1997), Illinois (Caton 1877), Texas (Derr 1990), Wyoming (Guiroy et al. 1991, E. S. Williams, in litt.), and Alberta, Canada (Lingle 1992, W. D. Wishart, in litt.). Whitehead (1972) reported white-tailed \times black-tailed deer hybrids produced in captivity in Tennessee.

Hybridization between white-tailed deer and mule deer has been documented genetically or on the basis of metatarsal gland morphology in the wild in Arizona (Day 1964, P. A. Dratch, in litt., J. A. Holcomb, in litt.), Montana (Cronin 1991), Texas (Carr et al. 1986, Stubblefield et al. 1986, Derr 1990, Ballinger et al. 1992), Washington (Gavin & May 1988), Wyoming (Kay & Boe 1992), and in Alberta (Wishart 1980) and British Columbia (Cowan 1962), Canada. White-tailed deer and mule deer are sympatric in the vicinity of the type locality of *crooki* (Hoffmeister 1962; A. Hurt, pers. comm.), and hybrids are documented from adjacent areas in Arizona and Texas.

The only genetic tests that will differentiate white-tailed deer and mule deer are electrophoresis of albumin (Scribner et al. 1984) and erythrocyte acid phosphatase (P. A. Dratch, in litt.), and isoelectric focusing of muscle esterase (Oates et al. 1979). All of these analyses require fresh or frozen samples. No molecular markers are currently known that will differentiate these species from skin samples from museum specimens (P. A. Dratch, in litt.).

Known hybrids are large and some body (length of ear and total length) and cranial measurements (zygomatic breadth, length of nasals, and upper and lower molariform toothrows) are within the normal range for desert mule deer (G. I. Day, in litt.). The phenomenon of heterosis (hybrid vigor) in F₁ hybrids is well known in cervids (Krzywinski 1993, Tate et al. 1997). The deer farming industry has capitalized on heterosis by crossing the phenotypically diverse, but presumed conspecific, red deer and wapiti (*Cervus elaphus*). F_1 hybrids show higher and faster weight gains making them more profitable than either purebred parental stock (Pearse 1993). Variability in overall size of F_1 phenotypes means that most cranial and body measurements are poor choices for evaluating hybrid status in deer (Cowan 1962; Day 1980, in litt.; Wishart 1980).

Any mule deer may have an abnormal tail, metatarsal gland, lacrimal fossa, cranial measurements, or length of hind foot. However, many characteristics from the type specimen for crooki fall outside the normal range of variation for mule deer, and are consistent with those of known white-tailed \times mule deer hybrids. The overwhelming concordance of morphologic evidence in this comprehensive analysis reveals the holotype of Dorcelaphus crooki as a hybrid between Coues white-tailed deer and desert mule deer. This, then, has serious repercussions for the current scientific name for desert mule deer. A scientific name based on a type specimen later found to be a hybrid is invalid and can not be used for either of the parental species even if it has priority over all other available names (ICZN 1985: Art. 23[h]). This reanalysis clarifies the long-standing confusion regarding the status of this contentious type specimen and therefore the correct scientific name for this taxon. The oldest available name for desert mule deer (formerly known as O. h. crooki and O. h. canus) is Odocoileus hemionus eremicus Mearns, 1897; an abbreviated synonymy follows:

Odocoileus hemionus eremicus (Mearns)

- Dorcelaphus crooki Mearns, 1897:2; unavailable name because it is based on a hybrid.
- Dorcelaphus hemionus eremicus Mearns, 1897:4; type locality "Sierra Seri, near the Gulf of California, in the most arid portion of Sonora, Mexico."
- Odocoileus hemionus canus Merriam, 1901:560; type locality "Sierra en Media, Chihuahua, Mexico."
- Odocoileus hemionus crooki: Goldman & Kellogg, 1939:507; name combination.

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Appendix 1 Specimens Examined

With the exception of the two type specimens of mule deer (both males) listed below, specimens used in this analysis, including the type of *Dorcelaphus crooki*, are all adult females (≥ 2 years), and deposited in the following institutions: Arizona State University (ASU); Arizona Game and Fish Department, Tucson (AGFD); University of Arizona (UA); National Museum of Natural History (USNM). A. L. Gardner measured the USNM specimens; I measured all others.

Odocoileus hemionus crooki [=eremicus] (14).— United States. Arizona: Yavapai Co., 8 km NE Horseshoe Dam (ASU 643); Maricopa Co., 3 km E Horseshoe Dam (ASU 637); Pinal Co., N side of Canyon Lake (ASU 643), Picacho Mountains (UA 24418– 24420, 24429, 24430, 24436, 24478, 25299, 25308). Mexico. Chihuahua: Sierra en Medio (USNM 99361, type of *O. h. canus*). Sonora: Sierra Seri (USNM 63403, type of *O. h. eremicus*).

Odocoileus virginianus couesi (17).—United States. Arizona: Cochise Co., Chiricahua Mountains (UA 20340, 20346); Graham Co., Blue River (USNM 32115); Pima Co., Santa Rita Mountains (AGFD 10, UA 23304), Baboquivari Mountains (AGFD 53201); Santa Cruz Co., Santa Rita Mountains (USNM 202931). New Mexico: Catron Co., Mogollon Mountains (USNM 148574); Grant Co., 32 km W Silver City (USNM 286685), head of Mimbres River (USNM 147476); Hidalgo Co., near Cloverdale (USNM 35748). Mexico. Chihuahua: Colonia Garcia (USNM 99347, 99350); Sonora: San Luis Mountains (USNM 35751, 37085); Pozo de Luis (USNM 59229).

Odocoileus hemionus crooki $[=eremicus] \times O.$ virginianus couesi hybrids (2).—Arizona: Pima Co., University of Arizona Captive Facilities (UA 22358). New Mexico: Hidalgo Co., Summit of the Dog Mountains (USNM 20572/35752, type of *Dorcelaphus crooki*).